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Impact of climate change on the transition of Neanderthals to modern humans in Europe

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Two speleothem stable isotope records from East-Central Europe demonstrate that Greenland Stadial 12 (GS12) and GS10—at 44.3–43.3 and 40.8–40.2 ka—were prominent intervals of cold and arid conditions. GS12, GS11, and GS10 are coeval with a regional pattern of culturally (near-)sterile layers within Europe's diachronous archeologic transition from Neanderthals to modern human Aurignacian. Sterile layers coeval with GS12 precede the Aurignacian throughout the middle and upper Danube region. In some records from the northern Iberian Peninsula, such layers are coeval with GS11 and separate the Châtelperronian from the Aurignacian. Sterile layers preceding the Aurignacian in the remaining Châtelperronian domain are coeval with GS10 and the previously reported 40.0- to 40.8-ka cal BP [calendar years before present (1950)] time range of Neanderthals' disappearance from most of Europe. This suggests that ecologic stress during stadial expansion of steppe landscape caused a diachronous pattern of depopulation of Neanderthals, which facilitated repopulation by modern humans who appear to have been better adapted to this environment. Consecutive depopulation–repopulation cycles during severe stadials of the middle pleniglacial may principally explain the repeated replacement of Europe's population and its genetic composition.

Central Europe | speleothems | millennial-scale climate cycles | stable isotopes | Middle–Upper Paleolithic transition

The replacement of Neanderthals by modern humans is recorded across Europe in a diachronous and culturally complex succession of distinct stone tool assemblages from the Middle–Upper Paleolithic transition (MUPT) roughly between 48 and 36 ka cal BP [calendar years before present (1950)] (1, 2). The succession often includes a regionally distinct “transitional” assemblage of local origin, or an intrusive Initial Upper Paleolithic assemblage between the Neanderthal Mousterian and modern human Aurignacian. The oldest anatomically modern human remains from Europe—found in East-Central Europe and radiocarbon dated to 40.6–38.6 ka cal BP (68% probability) toward the time of Neanderthals' disappearance from most of continental Europe—carry genetic evidence for species interbreeding four to six generations earlier (3–6). This individual, however, represents a population that did not contribute to the genome of modern humans present in glacial Europe after the MUPT (7), and the archeologic record provides no site with indication of local coexistence. Within a few millennia after the MUPT, at least two other genetically distinct modern human populations came to subsequently dominate Middle Pleniglacial Europe. During the entire interval, northern hemispheric climate went through several millennial-scale Dansgaard–Oeschger (DO) cold cycles (8, 9). A causality between climate change, the archeologic succession, and modern humans' genetic makeup has been tentatively suggested but not demonstrated (1, 2, 7). Below, we present the climatic history of continental Europe during the MUPT and derive the impact of climate change on MUPT demography, which may have led to the apparent repetitive genome turnover reported for Europe's human population during the middle pleniglacial.

The MUPT spans five DO cycles approximately between Greenland Interstadial 12 (GI12) and Greenland Stadial 8 (GS8) (9) for which climate change over continental Europe is poorly constrained. The paleoclimatic and environmental context is known with sufficient resolution and age-control only along the continent's western and southern fringe. In the Aegean and Black Sea region, records of sea surface temperature (10), coastal ice-rafted detritus (IRDC) (11), pollen assemblages (12–15), and stable isotopes in speleothems (16) suggest a DO-type response without the clear prominence of ice-rafting intervals (Heinrich stadials) seen in the Atlantic domain (17). Forest was generally more abundant in Europe during interstadials, while steppe landscape advanced during stadials (12). A taiga and tundra shrub/forest landscape covered the eastern European plains, with some loess deposition east of the Carpathians (12, 18, 19). The middle and lower Danube Plain was a steppe landscape with continuous loess deposition (20). A temperate open forest in the mountains of the southern Balkan passed into a xerophytic steppe toward the Aegean Sea (12, 13, 15). Boreal forest with birch and pine trees was present at 50° N in Western Europe (Eifel maar lakes) but began to degrade after GI12, ~44.5 ka cal BP (21). Two sparsely dated records from the Western Carpathians (Safarka, Jablunka) suggest a dense taiga forest landscape (14). For the upper Danube Plain, pollen (Fürmoos) and loess/paleosol profiles (Willendorf II, Nussloch)

Significance

A causality between millennial-scale climate cycles and the replacement of Neanderthals by modern humans in Europe has tentatively been suggested. However, that replacement was diachronous and occurred over several such cycles. A poorly constrained continental paleoclimate framework has hindered identification of any inherent causality. Speleothems from the Carpathians reveal that, between 44,000 and 40,000 years ago, a sequence of stadials with severely cold and arid conditions caused successive regional Neanderthal depopulation intervals across Europe and facilitated staggered repopulation by modern humans. Repetitive depopulation–repopulation cycles may have facilitated multiple genetic turnover in Europe between 44,000 and 34,000 years ago.

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The authors declare no conflict of interest.

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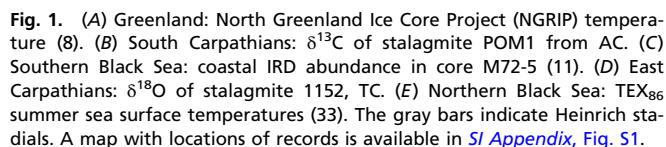
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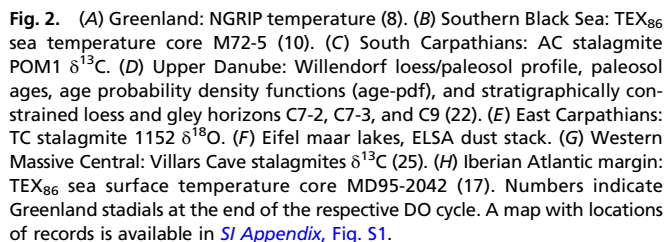
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The AC speleothem $\delta^{13}\text{C}$ record reproduces the DO pacing of the Greenland ice core record during the MUPT (Fig. 1). The TC $\delta^{18}\text{O}$ record reproduces some aspects of the Greenland record. The climatic meaning of the AC $\delta^{13}\text{C}$ data may be constrained within context of other records from the region, particularly the

The TC speleothem $\delta^{18}\text{O}$ record has an amplitude of $\sim 1\text{‰}$ and a different pacing compared with AC $\delta^{18}\text{O}$ (*SI Appendix, Fig. S3*). This suggests that the East Carpathians were in a different hydroclimatic regime during the MUPT. What defines the East Carpathian regime may be investigated by exploring the partial coherency between TC $\delta^{18}\text{O}$ and the other paleoclimate record. After ~ 60 ka, the $\delta^{18}\text{O}$ record shows low-amplitude variability with a few pronounced minima of $\sim 0.5\text{‰}$ that are coeval with some of the Greenland stadials (Fig. 1). These include GS3-H2, GS5-H3, and GS13-H5. Other minima just after 34 ka and at





Paleoclimatic Context of the Middle Pleniglacial in Europe

A reduction of forest and expansion of steppe biomes occurred during all stadials (12–15, 21), but climate records between the Atlantic and the Black Sea show a spatially heterogeneous response to DO cycles (Fig. 2). GS13–H5 is apparent in the TC speleothem $\delta^{18}\text{O}$ record but unlike in the Atlantic domain, its amplitude is small compared with subsequent stadials. Southern Black Sea IRDc data (Fig. 1) indicate less sea ice than during subsequent stadials despite apparent colder annual sea surface temperature (Fig. 2). This suggests a different seasonality with less severe winters. Thus, extreme cold was unlikely in East-Central Europe. The extreme aridity apparent in the Aegean region (13) may not have been as severe in the Balkan and Black Sea region (15, 16). GS12, from 43.4–44.3 ka_{GICC05} or 43.3–44.0 ka_{UT13b} (AC), is a very

prominent stadial in Greenland and Central Europe (Fig. 2), where permafrost changed the upper Danube lowland cold steppe into a tundra (see above). Malacological data from Willendorf II and the Eifel maar dust record suggests dryer conditions also in Western and Central Europe (22, 24) (Fig. 2). A cooling step likely occurred over Western Europe, supported by evidence of deep frost in the loess/paleosol record of northern France at ~43–44 ka cal BP (39). However, this stadial is less prominent in the Atlantic record (17). GS11 is present in all continental records, but not as pronounced as GS12. A common cooling trend superimposed over DO cycles 12–9 is apparent in all records (Fig. 2). GS10—from 40.1–40.9 ka_{GICC05} and 39.7–40.7 ka_{U-Th} (TC)—is a very prominent stadial over continental Europe, coeval with another cooling step in Western Europe (Fig. 2), but also a reduction in moisture and reduced speleothem growth (25). The first occurrence of loess in the Willendorf II profile (C7-2) around that time (22) and another strong dust peak in the Eifel maar record suggest stronger aridity than during GS12. Although present in all continental records, this stadial is unremarkable in the Atlantic and in the Black Sea (Fig. 2). However, annual sea surface temperature and winter coastal ice abundance in the Black Sea show conflicting results for GS10, which could again indicate a seasonality change. GS9–H4 is a long-lasting stadial that was less prominent in the Central European record but coeval with significant cooling and aridity in Western Europe (Fig. 2). Over the Atlantic and the Black Sea, GS9–H4 is a much more significant stadial. Subsequent GI8 is as warm as GI12 in Central Europe and the Black Sea region, with soil formation in the Danube region and East Carpathians (19, 20, 22), but colder in Western Europe and the Atlantic. Dust deposition in the Eifel maar records was also high during GI8, unlike GI13. The causes to this regionally heterogeneous response to DO climate cycles remain uncertain, but a variable influence of the Siberian high has been suggested (20).

Following the MUPT, GS8 from 36.6 to 35.5 ka_{GICC05} and GI7 from 35.5 to 34.7 ka_{GICC05} are difficult to separate from each other in the speleothem records. The Black Sea record shows severe cooling during GS8 (Fig. 2). The AC- $\delta^{18}\text{O}$ record suggests a significant fluctuation of the regional hydrologic condition during GS8 and GI7 in agreement with extended soil formation in the Danube Valley and the East Carpathians (19, 22). Higher moisture availability may have masked the temperature signal in AC- $\delta^{13}\text{C}$. After GI7, a long-term cooling trend is superimposed on DO variability throughout Europe (Fig. 2), in many places coincident with a long drying trend (20, 25).

The Relationship Between Demography and Climate Change During GS12 and GS10

GS12 and GS10 stand out as the most significant stadials in Central and Western Europe during the MUPT with severe cold, aridity, retreat of woodland, and expansion of steppe biomes. The consequence for human populations present is reflected in regional population decline (40) and in hunted game species, which in Western Europe changed from bovine dominated to reindeer dominated (41). Climatic and environmental constraints may not per se prove causality between the archeologic succession, the rapid replacement of humans' genome, and climate change, respectively. However, they do allow testing such a scenario for chronological feasibility: The biome changes during GS12 and 10 likely forced the population in open woodland habitats throughout Europe to adapt their subsistence strategy or habitat track their preferred biome to survive. Where biomes changed significantly, adaptation may not have been possible. During GS12 and 10, the permafrost boundary encroached the upper Danube region and East Carpathians. Both speleothems presented here suggest a rapid onset of stadial cooling and aridity in continental Europe within a few decades (Fig. 2). Depopulation would have been the consequence of failure to adapt or migrate away in time.

A number of chronologically well-constrained archeologic records allow for testing directly the feasibility of a regional depopulation scenario during severe stadials. Culturally (nearly) sterile layers have been reported—directly ^{14}C dated or constrained by ^{14}C -dated cultural layers above and below—in some regions and mark an archeological hiatus of several centuries duration. While such layers in some places represent short-term sedimentologic events without apparent discontinuity of habitation (42), at many sites their time span is multicentennial. These layers mostly relate chronologically to the time of GS12 and GS10, and suggest regionally widespread depopulation for many centuries between two subsequent cultures. (Fig. 3) (*SI Appendix, Table S2*). During GS12, this is the case for sites from the upper and middle Danube region. At Geissenklösterle, near-sterile (geologic) layer 17 separates Mousterian and Aurignacian assemblages (43) and is directly dated to 44.4–42.7 and 43.5–42.0 ka cal BP by two samples, with a Bayesian model age of 42.9–42.1 ka cal BP (44). At Sesselfelsgrötte, sterile layer F is directly constrained by Mousterian layer G1, 45.8–44.3 ka cal BP, and the late Mousterian layer E3, 42.2–40.5 ka cal BP, both recalibrated (4, 45). At Willendorf II, sterile layer C9 and subsequent layer C8-3 containing Aurignacian artifacts are constrained between two dated paleosols D1 and C8-2 (Fig. 2) (22). Mousterian Neanderthal presence in the middle Danube region has been redated to until ~45 ka cal BP, just before GS12 (46). Two sites with Aurignacian finds, at Keilberg-Kirche (47), 43.6–41.7 ka cal BP recalibrated (4), and at Pes-kő Cave, 43.8–41.2 ka cal BP (48), immediately postdate GS12. These fit the scenario of a cultural hiatus but lack local constraint by older assemblages. All of the above suggest widespread Mousterian Neanderthal

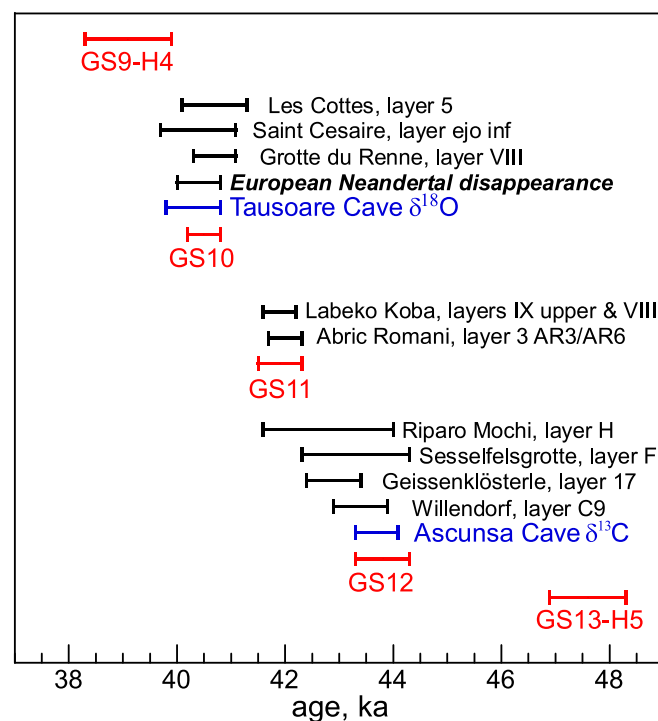


Fig. 3. The temporal pattern of Greenland stadials (red), prominent events in the Central European speleothem record (blue), and culturally (near-) sterile layers in archeologic records of Western and Central Europe (black). For stadials and speleothems, the bar shows the duration. For archeologic layers, the bar shows the 68% age interval (ka, cal BP) defined by the youngest date of the preceding layer and the oldest date of the succeeding layer. For details on archeologic radiocarbon chronologies, see *SI Appendix, Table S2*. A map with the locations of records is available in *SI Appendix, Fig. S1*.

depopulation of the upper and middle Danube Valley and—except for the tributary Altmühl Valley (49)—repopulation by Aurignacian after GS12.

Circumstantial evidence points to a similar impact of GS12 in northern Italy, where two sites, Riparo Mochi on the Ligurian Mediterranean coast—layer H—and at Grotta di Fumane in the Venetian Pre-Alps—layer A7—contain sterile layers probably coeval with GS12. However, reliable dating is only available for the base of the subsequent archeologic layer (50, 51) and age uncertainty is large (Fig. 3). A muted response to GS12 may be inferred for the site of Grotte Mandrin, Rhone Valley, where sterile layers separate strata C, B3, and B2 with post-Neronian-II artifacts (50). Layers B3–B1 of this latest regional Mousterian expression were dated in the range between 42.7 and 45.0 ka BP (6). These layers may indicate environmental change but do not appear to reflect longer breaks in the site's occupation. No such layers associated with GS12 are reported from archeologic sites further west. This suggests that the environmental impact of GS12 may have been less severe in Western Europe.

Sterile or near-sterile layers, or cultural hiatuses in the archeologic succession also occur around the time of GS10 (Fig. 3). This time is coeval with Neanderthals' disappearance from Western Europe (6). Sites include the Grotte-du-Renne—the low-density artifact layer VIII of intermittent Châtelperronian occupation (52); Les Cottés—sterile unit 5 (53); and Saint Césaire—layer Ejo inf (6). At Willendorf II, dated paleosols with lithic artifacts in C8 and C7 broadly constrain the sterile gley and loess horizons (C7-3 and C7-2) at that time (22) (Fig. 2). Subsequent archeologic layers are generally Aurignacian and document modern human expansion or reoccupation during GI9 and GI8 but under more arid conditions in Europe (Fig. 2).

A few archeologic profiles from around the Pyrenees—at Labeko Koba, Abric Romani, and possibly at Isturitz, but not at L'Arbreda (54–56)—contain sterile layers coeval with GS11 (Fig. 3). These represent a regional cultural hiatus between the Châtelperronian and the (Proto-)Aurignacian. However, apart from a long-term cooling and drying trend over Western Europe, an unambiguously dated climatic cold event cannot be detected in the present speleothem records for that time (Fig. 2).

A general case for likely adaptation of modern humans in response to climate change during the MUPT has already been made (48, 57, 58). Increasing cold and aridity around the onset of GS12 (Fig. 2) appears to mark transitions in the archeologic sequence attributable to Neanderthals that suggest some adaptation as well. GS12 is coeval with the transition from Mousterian to archaic Uluzzian, and then to evolved Uluzzian in northern Italy (59), and from Mousterian to Châtelperronian in Western Europe (53). However, late Neanderthals may have had a less diverse diet than modern humans (60). In open grasslands, Neanderthals' exclusive diet was meat from terrestrial animals, whereas modern human Aurignacian also exploited plant and aquatic foods (60, 61). The frequently observed cultural hiatuses, however, do not suggest a direct competitive displacement of Neanderthals, but rather a higher vulnerability to rapid environmental change and ecologic stress in the open landscape during cold and arid GS12–GS10. While Neanderthals did not

survive GS12 in most of the Danube steppe and tundra, modern humans may have been more capable to adapt and habitat track the expanding steppe in Central Europe. GS10 likely caused a repeat of that process in Western Europe.

A depopulation scenario was suggested for GS13–H5 as a trigger for the first intrusion of modern humans into Europe, represented by the Bohunician stone tool assemblage in Moravia (Central Europe) and further east (13, 62). Because a potential cultural hiatus is difficult to prove in the archeologic record of Moravia at given accuracy and precision of applied radiometric dating methods (63), this scenario may not currently be tested. There is also not as strong a climatic evidence in support. Cooling likely was less severe in East-Central Europe compared with subsequent stadials (see above). Severe aridity was apparent between the northern Aegean coastal region and the Levant (13, 64) but not over the Balkan (15), the Adriatic and the Black Sea regions (16, 65), or Central-East Europe.

The Moravian record suggests contemporaneity of modern humans—the Bohunician—and Neanderthals—the Szeletian—at close geographic proximity during GI12 and perhaps later but with some chronologic uncertainty (63, 66). During GI11–10, the situation is comparable for the Aurignacian and Mousterian on the upper Danube—at Keilberg-Kirche and Sesselfelsgrötte (see above)—and for Aurignacian and Szeletian on the middle Danube—at Pes-kő Cave and Szeleta Cave (42, 67) (*SI Appendix, Fig. S1*). Here, however, the interbreeding between species only six generations before the lifetime of the Oase Cave modern human specimen in that time range (5) principally confirms true contemporaneity along the northern fringe of the steppe landscape in the Danube Valley. Nonetheless, in the subsequent ~6 millennia after GS10, the modern human genome in Europe was replaced twice with a different genetic lineage harboring a much older Neanderthal ancestry (7). One modern European genetic branch found inside Goyet Cave (Belgium), was attributed to the late Aurignacian and dated to ~35 ka cal BP—coeval with GI7. This interval of modern human repopulation may have followed the extended cold interval from GS10 to GS9–H4, over 4,000 y long and only interrupted briefly by the 250-y-long GI9 (Fig. 2). A different genetic branch then dominated Europe after ~34 ka cal BP—coeval to the end of the severe and 1,000-y-long GS7 (Fig. 2). This lineage was attributed to the Gravettian (7), who repopulated Europe during yet another time of low population density (68). The discussion above lays out a general scenario of depopulation–repopulation cycles associated with steppe landscape expansion following extreme or long stadials. The comparable timing of stadials and population changes seen in the archeologic and genetic record suggests that millennial-scale climate cycles may have been the pacesetter for Europe's demographic history during the Middle Pleniglacial.

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